

## NON-BREEDING TERRITORIALITY OF SEMIPALMATED SANDPIPERS

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ABSTRACT.—We studied non-breeding territorial behavior of Semipalmated Sandpipers (*Calidris pusilla*), and documented the proportion of individuals of Least (*C. minutilla*) and Western (*C. mauri*) sandpipers exhibiting territoriality during fall of 1994 and 1995 at the Cabo Rojo salt flats, Puerto Rico. Territoriality was exhibited by 8–19% of the population, with Least Sandpipers exhibiting the highest proportion of all three species. The prevalence and size of territories of Semipalmated Sandpipers was influenced by the availability of high prey density sites, bird density, and aggression levels. Individuals defended territories in areas of highest prey densities ( $0.16 \pm 0.009 /\text{cm}^3$ ). Non-territorial birds, however, foraged in areas of significantly higher prey densities ( $0.02 \pm 0.001 /\text{cm}^3$ ) than overall lagunal levels (i.e., randomly sampled plots) ( $0.006 \pm 0.009 /\text{cm}^3$ ). Territorial Semipalmated Sandpipers spent less time foraging than non-territorial birds (1994: 90 vs 36%; 1995: 85 vs 55%). They also spent less time in maintenance behavior (i.e., preening). Costs of territoriality may be offset by foraging in areas of high prey densities or through increased foraging efficiency. Prey density did not exert a direct influence on territory size ( $P = 0.67$ ). Rather, it influenced territory size through effects on aggression. Territory size was inversely related to the mean time spent on aggression ( $P < 0.001$ ). Territory size was also inversely related to bird density ( $P < 0.001$ ), a factor that might contribute to higher incidence of aggressive bouts. These findings support the contention that a facultative strategy with respect to non-breeding territorial behavior seems to offer migratory species the flexibility to cope with spatio-temporal fluctuations of prey resources and shorebird density. Received 12 Nov. 1996, accepted 22 April 1997.

Migratory shorebirds spend over half of their annual cycle at staging areas and wintering grounds (Gochfeld et al. 1984). During this period, they must satisfy high energetic demands (e.g., molt, migratory flights) in the face of variable environmental conditions (e.g., food resources, weather, predation) (Pienskowski and Evans 1984, Senner and Howe 1984, Myers et al. 1987). These conditions may increase the risk of mortality, justifying emphasis on the migratory and wintering periods in discussions of shorebird population regulation (Myers et al. 1985, Myers et al. 1987). Shorebirds have developed several strategies to cope with such energetic demands. At a hemispheric level, they rely on a few vital links that serve as resting and foraging areas (Myers et al. 1987). At a local level, shorebirds distribute themselves where prey items are most abundant (Hicklin and Smith 1984, Gear 1992). Within these patches, some shorebird species select the most energetically profitable prey items (e.g.,

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by size or prey type) (Goss-Custard 1970, 1977; Goss-Custard et al. 1977). Furthermore, if prey are defendable, some individuals will assert exclusive claim over food resources through territorial behavior (Brown 1964, Recher 1966, Myers et al. 1979a).

Territoriality in non-breeding shorebirds has been documented at migratory stopovers and wintering areas in northern latitudes (Hamilton 1959, Myers 1979a, Connors et al. 1981) as well as on their tropical wintering grounds (Duffy et al. 1981, Myers and McCaffery 1984). Yet, despite its widespread occurrence, the benefits of engaging in non-breeding territorial behavior are not well understood (Myers et al. 1979a, Myers 1984). Costs associated with the establishment and maintenance of territories are high, sometimes at the expense of essential activities such as foraging and maintenance. It is believed that territorial individuals attain a higher net energetic gain than non-territorial shorebirds (Brown 1964, Verner 1977); however, there has been no conclusive evidence to support this contention (Myers et al. 1979a, Myers 1984). The trade-offs between energetic gains and costs of territorial defense can be reflected in the variability of territory size (Myers et al. 1979b). For instance, Myers (op. cit.) showed that Sanderlings (*Calidris alba*) will defend an area as large as competition permitted. This finding suggested that prey density was not the sole determinant of territory size as previously hypothesized (Stimson 1973, Brown 1975, Gass et al. 1976). Myers et al. (1979b) demonstrated that territory size varied inversely with prey density. The inverse relationship resulted from the determining influence of an intervening factor, intruder density. Unfortunately, lack of information on other species precluded Myers et al. (1979b) from making generalizations about their territory size model.

Identifying components of non-breeding territoriality shared among species is necessary to gain insights about its possible adaptive significance. Meeting this need has been hampered by the dearth of information on non-breeding territoriality. In this study, we test whether Myers' et al. (1979b) model of Sanderling non-breeding territoriality is applicable to Semipalmated Sandpipers (*Calidris pusilla*) at the Cabo Rojo salt flats, Puerto Rico. Specifically, we tested whether prey density had a regulatory effect on territory size or whether territory size was mediated by intruder density. Other components of non-breeding territoriality were examined in order to develop a broader base for generalizations and aid in the interpretation of costs and benefits of territoriality. To this end, we tested or documented (1) whether prey densities on defended territories differed significantly from those on adjacent areas where territoriality was not exhibited, (2) the allocation of time to selected activities by territorial and non-territorial individuals, and (3) the prevalence of territorial individuals

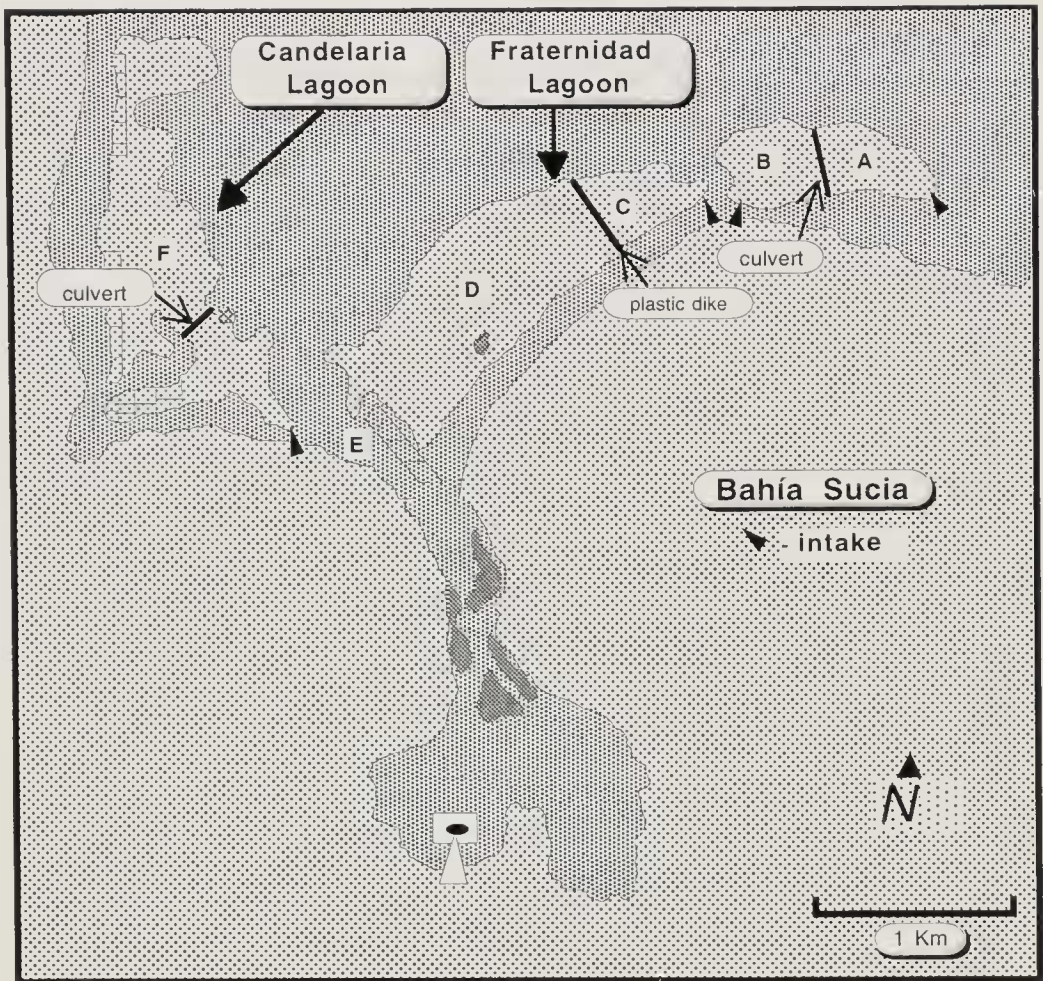


FIG. 1. Map of the Cabo Rojo salt flats, Puerto Rico showing sampling areas (A–F) in the Fraternidad and Candelaria lagoons. Shorebird observations were made along the north-west shore of area A (1994) and the north shore of area D (1995).

in the population, including observations on Least (*Calidris minutilla*) and Western (*Calidris mauri*) sandpipers.

#### STUDY AREA AND METHODS

This study was conducted at the Cabo Rojo salt flats in southwest Puerto Rico ( $67^{\circ}12' N$ ,  $18^{\circ}57' W$ ) (Fig. 1). Two large shallow lagoons, Fraternidad and Candelaria, covering approximately 445 ha are the most striking features of the area. Strips of littoral vegetation, dirt, and paved roads delineate most of the salt flats and roads provide access to nearly every location. Mean ( $\pm SE$ ) water depth (cm) per area was  $5.3 \pm 0.2$  (A),  $5.7 \pm 0.2$  (B),  $16.2 \pm 0.5$  (C),  $15.3 \pm 0.4$  (D), and  $16.2 \pm 0.4$  (F) (Fig. 1). Size (ha) estimates of sampling areas were A (17.4), B (19.0), C (72.3), D (10) and F (26.2). Data presented herein were collected in areas A and D of Fraternidad Lagoon. These areas encompassed the range of salinity levels in the system, hosted two primary prey species, and were accessible (i.e., depth range) to foraging Calidrids (Gear 1992, Tripp 1996). Prey species were water boatmen (*Trichocorixa reticulata*), found exclusively in area A, and brine shrimp (*Artemia* spp.), found only in area D.

Observational data were collected on the north shore of area D from September 8 through 25, 1995. The shoreline was divided into seven 100 m strip sections identified either by stake markers or landmarks. Each day, a section of shoreline was randomly chosen for observations. We stood 50 m from the left end of the selected section and used focal and scan sampling to collect behavioral information (Altmann 1974). Scans were used to determine the proportion of birds in the flocks engaged in territorial behavior. Focals were used to determine the percentage of time selected individuals were engaged in distinct behaviors. We initiated observation periods with a scan of the selected sampling area, recording species composition, numbers of small calidrids, and the number of territorial birds with the aid of binoculars. Shorebirds were considered territorial if they exhibited behaviors such as vigilance in response to potential intruders or aggressive displays associated with boundary disputes. Upon completing the scan, we selected the first territorial bird (i.e., focal) looking from left to right within the area of interest and recorded the total number of shorebirds within a 10 m radius of the focal individual. We then recorded the focal bird's behavior for a total of three minutes (Ashmole 1970). Behaviors were classified according to the following categories (adapted from Hamilton 1959): vigilance (alert posture with neck stretched upwards and legs straightened), aggression (threat posture with head down and rump raised, or an attack where a bird either rushes across the ground or flies at an opponent, displacement (the act of a bird chased away from a location), foraging (searching, handling and ingestion of prey), and preening (cleaning its feathers).

Territories were linearly arranged along the shoreline with widths not exceeding 1 m. Territory dimensions were estimated on the basis of the locations of other birds which elicited an aggressive stance or attack from the territorial bird (Myers et al. 1979b). After completing the focal sample, we selected the first non-territorial bird seen  $\geq 2$  m into the lagoon from the territorial bird. Non-territorial birds were usually found away from the shoreline in deeper waters. We then collected data in the same manner and also added the behavioral category of displacement. After completing observations on a pair of territorial and non-territorial birds, we shifted our observation focus 10 m down the shoreline and selected the next territorial bird. If any focal birds left the area before the 3-min period ended, we omitted the observation and selected another individual.

The location of each focal bird was carefully noted using stakes placed in the lagoon or other landmarks used as reference points. After every three paired observations of territorial and non-territorial birds, we sampled prey at each location. Sandpipers were observed foraging only in the water column (Tripp 1996) to which we restricted prey sampling. Prey were sampled using a plastic cylinder 15 cm in diameter. Upon approaching the area of interest (i.e., first location noted for each focal), we extended our arms (0.5–0.9 m from our torso), dropped the cylinder and pushed it into the substrate to minimize prey loss. We then measured the depth of water, filtered the trapped water through a 1 mm mesh sieve (Bengston and Svennson 1968), and counted and identified the types of organisms within the sampled volume of water. After this process was completed, we initiated another set of three paired observations of territorial and non-territorial birds, starting from the point along the 100 m transect where the last set of observations was made. For each 100 m strip of shoreline, a total of nine sets of paired observations were made, each with respective data on prey availability. Estimates of lagunal prey levels were obtained from four sampling plots established throughout area D (Tripp 1996). Plot dimensions were 50 m  $\times$  30 m. Each plot was divided into six divisions along the shoreline and three subdivisions perpendicular to the shoreline. Every plot was sampled once a week. Each week, two divisions were selected randomly. From each selected division, two samples from each of two randomly chosen subdivisions were collected. Subdivisions were sampled without replacement. Prey was processed as described above for territorial and non-territorial locations. In all cases, it is

possible that prey estimates were biased low (e.g., prey moving away from approaching sampler); however, sampling was standardized, and thus comparisons were made on the basis of precise estimates.

From September to November 1994 behavioral data were also collected on the northwest shoreline of area A. This area was divided into five  $50 \times 10$  m sections. Each day a section was randomly chosen. Scan and focal behavioral data were collected as in 1995. Differences between years were in the number of scans performed and how the focal bird was selected. In 1994, scans were done every hour. Focal birds were selected by focusing binoculars in the center of the observation area and selecting the bird to the right of the center of the field of view. Subsequent focal birds were selected by choosing an individual about 10 m to the right or left of the previous focal bird to minimize observing the same bird.

A paired *t*-test was used to test whether there were differences in prey density (individuals/cm<sup>3</sup>) or bird density between territorial and non-territorial sites. Unless otherwise specified, bird density is defined as number of birds within a 10 m radius of focal birds. The 10 m was estimated with the aid of stakes and landmarks in the observation area. Territory sizes (m) (i.e., linear dimension) between areas A and D, and percent of time spent by territorial and non-territorial individuals on selected behavioral categories were compared using Wilcoxon tests (JMP 1994). Because shorebird density can influence territory size (Myers et al. 1979b), comparisons between areas A and D were made only when the number of shorebirds per area were comparable (i.e., adjusting by density). Averages were reported as mean  $\pm$  standard error.

Path analysis was performed on 1995 data (sensu Myers et al. 1979b). To conduct the analysis, standardized values of the inverse of territory length (1/TL), the response variable, were regressed on the percentage of aggressive activity (AGG) and prey density (PD), the independent variables, using multiple regression. The inverse of "TL" was used because a hyperbolic relationship between prey density and territory size was expected (Gass et al. 1976, Myers et al. 1979b). The relationship between PD and AGG was determined using a simple regression analysis. Standardized regression coefficients indicate the strength of the relationships among the variables of interest (Mitchell 1993). Unlike Myers et al. (1979b), we used the mean total time spent in aggression as an index of territory defense (i.e., AGG) because shorebirds were not individually marked. Territorial birds attack or display towards trespassers in various ways, from short-lived threatening stances to prolonged physical attacks. Therefore, we believe that mean total time spent in aggression was a good indicator of the extent to which a bird defended a territory. Simple regression analysis was used to examine if the relationship derived from 1995 data between AGG and 1/TL was also observed in 1994. All tests were considered significant at an alpha of  $\leq 0.05$ .

## RESULTS

Semipalmated Sandpipers monitored in areas A and D accounted for 61% (1994) and 80% (1995) of the birds. Western Sandpipers and Least Sandpipers were second in abundance in 1994 and 1995, respectively. Within the flocks observed during the study, 8% to 19% of the birds exhibited territorial behavior (Table 1). On the average, Least Sandpipers comprised the highest proportion of territorial birds. Proportion of territorial birds varied markedly for Semipalmated Sandpipers between 1994 and 1995 but not for Western or Least Sandpipers.

Territories of Semipalmated Sandpipers consisted of rectangular strips along the shoreline, ranging from  $3.30 \pm 0.19$  m in 1994 ( $N = 53$ ) to

TABLE 1  
 MEAN ( $\pm$ SE) NUMBER PER SCAN SAMPLE OF LEAST (LESA), SEMIPALMATED (SESA) AND WESTERN (WESA) SANDPIPERS AT THE CABO ROJO  
 SALT FLATS, PUERTO RICO IN 1994 AND 1995

Year	Mean number per scan	Mean percent of total numbers by species			Mean percent territorial birds within a species <sup>b</sup>			
		LESA	SESA	WESA				
1994	126.6 $\pm$ 7.0	19.8 $\pm$ 2.9	60.8 $\pm$ 4.6	19.5 $\pm$ 4.8	8.5 $\pm$ 7.9	15.2 $\pm$ 4.9	5.3 $\pm$ 2.7	2.3 $\pm$ 0.6
1995	62.9 $\pm$ 0.9	16.6 $\pm$ 2.6	79.8 $\pm$ 3.7	5.7 $\pm$ 1.9	18.5 $\pm$ 0.9	12.4 $\pm$ 6.4	14.0 $\pm$ 3.8	4.4 $\pm$ 1.2

<sup>a</sup> Territoriality is expressed as the mean ( $\pm$  SE) percent of the total number of birds exhibiting territoriality.

<sup>b</sup> Territorial behavior broken down by species and expressed as the mean ( $\pm$  SE) percent of birds within a species exhibiting territoriality.

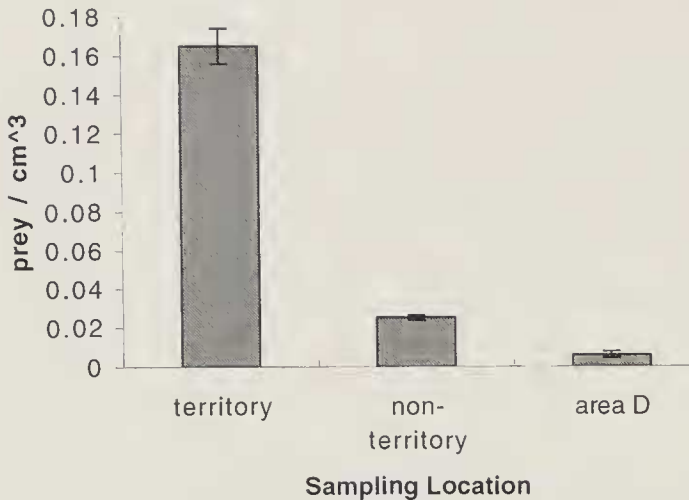


FIG. 2. Mean ( $\pm$ SE) brine shrimp/volume sampled in territory and non-territory sites of Semipalmated Sandpipers and randomly sampled plots in area D at the Cabo Rojo salt flats, Puerto Rico.

4.80  $\pm$  0.31 in 1995 (N = 55). Territory length was linearly but negatively related to bird density (1994-area A:  $F = 45.03$ , d.f. = 1, 51;  $P < 0.001$ ,  $R^2 = 42\%$ ; 1995-area D:  $F = 14.37$ , df = 1, 53;  $P < 0.001$ ,  $R^2 = 22\%$ ). Adjusting for bird density, territory length was not significantly different between areas ( $\bar{x}$  A = 5.00  $\pm$  0.85;  $\bar{x}$  D = 4.70  $\pm$  0.28;  $\chi^2 = 0.66$ ,  $P = 0.42$ ). Prey density levels in territories ( $\bar{x} = 0.16 \pm 0.009/\text{cm}^3$ ) were significantly higher than in areas where no territoriality was exhibited ( $\bar{x} = 0.02 \pm 0.001/\text{cm}^3$ ;  $t = -15.10$ , df = 64,  $P < 0.001$ ). Areas used by non-territorial birds had significantly higher prey densities than randomly sampled plots in area D ( $\bar{x} = 0.006 \pm 0.009/\text{cm}^3$ ;  $\chi^2 = 40.88$ ,  $P < 0.001$ ) (Fig. 2). Bird density within a 10 m radius of focal birds was significantly greater around non-territorial birds ( $\bar{x} = 17.36 \pm 1.12$ ) than territory holders ( $\bar{x} = 12.17 \pm 0.72$ ;  $t = 3.65$ , df = 56,  $P = 0.0006$ ).

Time spent on aggression by territorial Semipalmated Sandpipers ranged from 26% in 1995 to 47% in 1994 (Table 2). Time spent in aggression and density of birds were significantly and positively related (1994-area A:  $F = 18.96$ , df = 1, 51,  $P < 0.001$ ,  $R^2 = 27\%$ ; 1995-area D:  $F = 49.55$ , df = 1, 53,  $P < 0.001$ ,  $R^2 = 48\%$ ). As time spent in aggression increased, territory length decreased (1994-area A:  $F = 46.33$ , df = 1, 51;  $P = 0.001$ ,  $R^2 = 48\%$ ; 1995-area D:  $F = 82.63$ , df = 1, 53;  $P < 0.001$ ,  $R^2 = 61\%$ ). There was a significant inverse relationship between the number of territorial birds and the total number of birds counted within a 50 m  $\times$  10 m area ( $F = 6.84$ , df = 1, 13;  $P = 0.02$ ,  $R^2 = 35\%$ ) (Fig. 3). Territorial birds spent significantly less time foraging (1994:  $\chi^2 = 103.14$ ,  $P < 0.001$ ; 1995:  $\chi^2 = 55.23$ ,  $P < 0.001$ ) and preening (1994:  $\chi^2 = 9.19$ ,  $P = 0.002$ ; 1995:  $\chi^2 = 38.39$ ,  $P < 0.001$ ) than did non-

TABLE 2

MEAN ( $\pm$  SE) PERCENT OF TIME SPENT ON SELECTED BEHAVIORAL ACTIVITIES BY TERRITORIAL AND NON-TERRITORIAL SEMIPALMATED SANDPIPERS IN 1994 AND 1995 AT THE CABO ROJO SALT FLATS, PUERTO RICO

Behavior <sup>a</sup>	Territorial (N = 188)		Non-territorial (N = 115)	
	1994	1995	1994	1995
Aggression	47.4 $\pm$ 2.5	25.5 $\pm$ 1.5	0	0
Preening	0	0	6.9 $\pm$ 1.8	11.3 $\pm$ 2.1
Vigilance	17.4 $\pm$ 2.1	19.9 $\pm$ 2.2	0.5 $\pm$ 0.2	2.5 $\pm$ 0.9
Foraging	35.2 $\pm$ 2.7	54.5 $\pm$ 2.2	89.8 $\pm$ 1.95	85.1 $\pm$ 2.2
Displacement	0	0	2.81 $\pm$ 0.8	1.0 $\pm$ 0.5

<sup>a</sup> Percentages estimated on the basis of 3-min focal samples. Behavioral activities adapted from Hamilton (1959).

territorial birds in both years (Table 2). Conversely, they spent more time in vigilance than non-territorial birds (1994:  $\chi^2 = 97.62$ ,  $P < 0.001$ ; 1995:  $\chi^2 = 41.93$ ,  $P < 0.001$ ) and were the only individuals to exhibit aggression.

Aggression (AGG) had a strong effect on territory size (1/TL) (stand. partial coef. = 0.82,  $df = 1$ , 52;  $P < 0.001$ ,  $R^2$  for multiple regression = 71%) (Fig. 4). Similarly, prey density had a strong effect on aggression (stand. coef. = 0.60,  $P < 0.001$ ,  $R^2 = 39\%$ ). In contrast, prey density had little effect on territory size (stand. partial coef. = 0.04,  $df = 1$ , 53;  $P = 0.67$ ). The relationship between 1/TL and AGG in 1994 was consistent with the relationship found in 1995, that is, they were linearly and



FIG. 3. Number (and percentage) of territorial Semipalmated Sandpipers recorded at different bird densities at the Cabo Rojo salt flats, Puerto Rico, in 1994 and 1995.



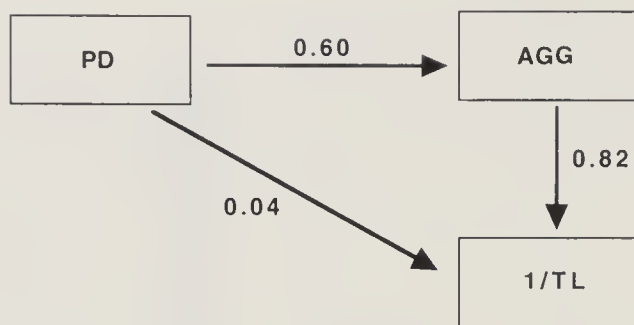


FIG. 4. Path diagram showing the relationship between prey density (PD), mean total time spent on aggression (AGG), and territory length (TL) exhibited by Semipalmated Sandpipers at the Cabo Rojo salt flats, Puerto Rico. Path coefficients are standardized partial regression coefficients predicting  $1/TL$  from PD and AGG. Path coefficient predicting AGG from PD is a standardized regression coefficient.

positively related (stand. partial coef. = 0.69,  $df = 1, 51$ ;  $P < 0.001$ ,  $R^2 = 48\%$ ).

#### DISCUSSION

Areas held by territorial Semipalmated Sandpipers had significantly higher prey densities than areas held by non-territorial birds, and foraging sites used by non-territorial birds had higher prey densities than randomly sampled lagunal plots. These findings were consistent with the hypothesis that shorebirds should distribute themselves according to the prey density distribution (see Hicklin and Smith 1984). Findings also indicate two levels of habitat selection. Food was most abundant where flocks of birds occurred (i.e., mix of territorial and non-territorial individuals), as compared to randomly sampled plots in area D. A similar pattern was reported by Grear (1992). Moreover, territorial birds selected prey patches at a scale which hosted the highest overall prey density. This suggests that territorial birds defend patches of abundant food resources which might confer unique energetic benefits to the territory holder (Brown 1964, Myers et al. 1979a).

The relationship among territory length, aggression, and prey density suggests that inferences made by Myers et al. (1979b) for Sanderlings can be extended to include Semipalmated Sandpipers. Accordingly, our findings support the hypothesis that this species will defend territories as large as competition permits. Prey density did not exert a strong effect on territory size. The weak relationship had its basis in the fact that levels of aggression increased in areas of highest prey densities, likely due to the fact that bird density also increased with prey density. As bird density increased, the number of territorial birds decreased significantly. This relationship was true both for brine shrimp (area D) and water boatmen

(area A). Similar findings have been documented for Great Tits (*Parus major*), where year to year variation in territory size is related to the number of birds seeking territories rather than variations in prey density (Krebs 1971).

Myers et al. (1979a) identified three concurrent levels of prey density and documented territoriality only at intermediate levels. They hypothesized that at higher prey densities (e.g., superabundant resources) territories could not be defended due to the high frequency of intrusions caused by the higher concentration of shorebirds (see also Brown 1964). Consistent with Myers et al. (1979a) findings, we found expressions of territoriality lessened with increasing bird density. Decreasing territoriality, however, was not associated with a third level of prey density (e.g., superabundant). We only identified two levels of prey density, with territoriality always associated with areas of highest densities. As birds discovered these sites, their densities increased to levels where territorial defense was no longer possible. Further evidence that a superabundant level of prey abundance was not present at the salt flats was that the highest bird densities were associated with non-territorial birds. These birds foraged in areas of lower prey densities than territorial birds, albeit not as low as the overall background levels (i.e., random samples) in the salt flats. Differences between Myers (op. cit.) findings and our study may be accounted for by differences in prey species and system productivity.

Our findings raise questions about the adaptive significance of non-breeding territoriality, as did those of Duffy et al. (1981, 1984) and Myers (1984). Territory holders have nearly exclusive access to higher than average prey concentrations. To gain this privilege, however, they spent large amounts of time on aggression and vigilance and reduced preening time. Possibly, prey intake is increased to compensate for lost time in aggression and vigilance (Mallory and Schneider 1979, Goss-Custard 1984). Studies of marked populations (i.e., Sanderlings, Myers et al. 1979b), however, also suggest that not all individuals are territorial, and those that are exhibit a great deal of variability in their expression of it (e.g., hours to months). This suggests that territoriality is not the only strategy that migrant shorebirds use to meet their energetic demands and that energetic gains derived from territoriality could be accrued by a mix of short and long-term bouts. When territoriality is not possible, individuals could draw upon the extra time not invested in territorial defense to ensure adequate energy-intake and maintenance. The persistence of this alternative strategy in the population probably has its basis in the ability of non-territorial individuals to maximize their energy intake by foraging in areas that, although not as good as terri-

tories, still have relatively higher prey concentrations than randomly sampled plots as shown in this study.

Why is non-breeding territoriality not more prevalent in the population? In the salt flats, the proportion of territorial individuals of three species of small calidrid sandpipers ranged from 8–19%. One possibility is that while being territorial might yield greater benefits, establishing territories can occur only at certain levels of prey density. Moreover, if the area where such conditions prevail is spatially limited, the number of territories would be constrained as well. Our observations were consistent with these possibilities. Territoriality was observed only in a few shoreline locations with relatively high concentrations of prey. These patterns could be explained, in part, by the resultant effect of prevailing winds (i.e., east, south-east) and their variable speeds which accumulated prey along the shoreline region (Tripp and Collazo 1995). Our observations suggest that shifts from territoriality to vagility (i.e., longevity of territories) were likely adjustments to spatio-temporal fluctuations in resource availability (Connors et al. 1981, Duffy et al. 1981, Myers 1984).

Least Sandpipers consistently exhibited more territoriality than did Semipalmated or Western sandpipers. This pattern is interesting because Least Sandpipers are restricted to shallow waters by virtue of their size (2 cm tarsometatarsus). As such, they often forage amidst dense, mixed-species flocks. Aside from species-specific differences in behavior, higher expressions of territoriality were probably facilitated by their relatively low numbers and the fact that Semipalmated and Western sandpipers can scatter themselves over a wider range of foraging depths, hence, minimize the potential number of intrusions into territories. Least Sandpipers might also be responding to patterns of prey composition and dispersion along the wet and submerged transition zone of shorelines not found in deeper waters exploited by Semipalmated and Western Sandpipers.

Hypothesized benefits and costs of non-breeding territoriality need to be judged on the basis of demographic effects (e.g., survivorship rates) and population regulatory functions (Myers 1984). Information on the former is lacking and evidence for the latter is equivocal (Duffy et al. 1981, 1984; Myers 1984, Myers and McCaffery 1984). There is agreement, however, that migrant shorebirds face high energetic demands (Myers 1984, Myers et al. 1987). The findings of our study support Connors' et al. (1981) contention that a facultative strategy with respect to non-breeding territorial behavior seems to offer migrant shorebirds the flexibility to cope with spatio-temporal fluctuations in resource availability and bird density.

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